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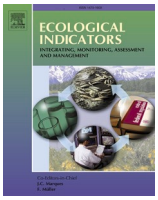

Interspecific relationship of patchiness to occupancy and abundance, as exemplified by seagrass macrobenthos

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ABSTRACT

The macroecological abundance-occupancy relationship is well known; not so the potential one of patchiness with either or both. Following earlier work on the intertidal seagrass *Zostera capensis* in South Africa, interspecific macrofaunal patchiness-occupancy and patchiness-abundance relationships were investigated within each of a number of other seagrass systems (intertidal *Cymodocea serratula*, *Halodule uninervis*, *Halophila ovalis*, *Zostera muelleri* and *Z. noltei*, and subtidal *Z. capensis*) where faunal assemblages were markedly different in their overall abundance and species richness, and where the beds differed in their latitude, longitude, and other variables, including one in an artificial canal in a residential marina. Notwithstanding these differences, in all cases the more abundant and widespread the macrobenthic species, the less was its Lloyd's I_p patchiness, the more clearly so in respect of occupancy than of abundance. Correlation of I_p and mean crowding (I_c) values was relatively poor, and often not significant. This suggests that patchiness of a species is more influenced by unoccupancy levels than by even marked variation in abundance at occupied sites (e.g. I_c values of <0.3–>380). Indeed, values of I_p were closely correlated with the expression [a.unoccupancy + (1−a).I_c], where a is >0.80. In all cases, component macrofaunal species displayed a significant or near significant negative patchiness-occupancy relationship in the form of a power-law with a mean scaling coefficient across sites of −0.76, although data points appeared highly scattered. There was little uniformity amongst the component species in the life-style of the most patchy, most widespread or most abundant.

1. Introduction

It is a well attested phenomenon, and arguably the most pervasive of ecological 'rules', that the abundance of a species (number of individuals per unit area) is closely and positively related to its occupancy (probability of occurrence in unit sample) (Gaston, 1996; Gaston et al., 2000; Roney et al., 2015; etc.). Thus if, for each of the component species in a given assemblage, interspecific log abundance is plotted against log occupancy, a straight-line or curvilinear relationship is obtained across the whole assemblage following a power-law pattern (He and Gaston, 2003). Causality is still debated and a considerable number of different models have been proposed in explanation (Holt et al., 2002; Frisk et al., 2011; Webb et al., 2019; etc.). Such a relationship has, however, been demonstrated in all types of ecological system and for all types of organism investigated (although *c.f.* Bijleveld et al., 2018), including for the estuarine macrobenthos (Foggo et al., 2003) and that of intertidal seagrass (Barnes, 2019a, 2020). Further, He and Gaston (2003) and Gaston et al. (2006) have shown that the precise occupancy of a given species can be estimated with great accuracy solely from data on its abundance, specifically from its mean density and the variance displayed about that mean. Thus intraspecifically 'the abundance of a species, its spatial variation and the area of occupancy on landscapes are uniquely constrained, involving no further parameters' (Gaston et al., 2006:654). Assemblages of species will have properties constructed from those of their individual components, and Frisk et al. (2011), for example, produced intraspecific abundance-occupancy curves for each of the 32 sampled fin- and shellfish on the Georges Bank in the North Atlantic, and then calculated a global fit curve across all those species.

Spatial patchiness of abundance is another pervasive phenomenon that manifests across all ecological systems, including the seagrass beds of coastal marine waters (Healey and Hovel, 2004; Magni et al., 2017). Although 'ecologists have long regarded patchiness as a nuisance

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because of the high variance it imposes on sampling programmes' (Raffaelli et al., 2003:196), it has for some time been regarded as one of the most important attributes of benthic marine systems in its own right, leading Rufino et al. (2018), for example, to argue strongly for greater integration of spatial indicators into marine conservation and species ecology. But whilst the effect of patchiness of the habitat on its associated fauna has received much attention (Eggleston et al., 1999; Healey and Hovel, 2004; Boström et al., 2006; Lefcheck et al., 2016; Staveley et al., 2017), patchiness of individual species and of whole species assemblages across apparently non-patchy habitat has been largely ignored (although see Kraan et al., 2009). Recently, however, Barnes (2019a) sought to incorporate such within-habitat patchiness of the fauna into the abundance-occupancy relationship, investigating a large dataset of the dominant invertebrates comprising the benthic macrofauna of each of a disparate series of non-fragmented intertidal beds of Cape dwarf-eelgrass, *Zostera* (*Zosterella*) *capensis*, across a wide range of seagrass habitat types in the Knysna estuarine bay, South Africa. He showed that equivalent interspecific power-law relations also existed between occupancy and patchiness of the dominant faunal species at Knysna, spatial patchiness being assessed as Lloyd's index of patchiness, I_p. However, no significant interspecific relationship between abundance and patchiness was found in any of these assemblages notwithstanding the close correlation between abundance and occupancy. The Knysna seagrass system displayed an abundance-occupancy-patchiness pattern in which the more widely distributed a given species was across unit area, the less was its variation in density from point to point. To date this finding appears to be the only attempt specifically to relate patchiness in density across the component species of a marine macrobenthic assemblage to their overall abundance and/or occupancy, and the present study therefore sought to expand such analysis to a much broader range of conditions: to other species and genera of seagrasses, to geographical regions beyond South Africa's Indian Ocean coast, and to other tidal heights, to ascertain the generality of such relationships.

In light of the known relationship between occupancy and spatial variance in abundance demonstrated by He and Gaston (2003), it is perhaps necessary to stress at the outset that the words *spatial variation* in the quotation from Gaston et al. (2006) above are capable of being interpreted in more than one way. In the macroecological literature they refer specifically and only to *spatial variance*, not to *spatial patchiness*. The two concepts, although both concerning spatial variation in numbers, are quite different, and this research is not seeking to 're-invent the wheel' of the occupancy-spatial variance relationship: variance is, of course, a statistical concept (the squared deviation of individual values from their mean) whilst patchiness is the tendency to occur differentially in spatially distinct subunits within a given area, i.e. to show 'clumping', 'aggregation' or 'overdispersion', although such patchiness may also be quantified by expressions derived from the mean and variance of abundance. In fact, the difference between the two potential meanings of spatial variation is such that in the results described below at none of the 12 sites investigated was there any significant correlation between values of spatial variance and spatial patchiness (all $P > 0.1$).

2. Materials and methods

Historical datasets are available for the seagrass macrobenthos associated with six seagrass species from four genera in coastal localities in the British North Sea (northeastern Atlantic Ocean), the Knysna estuarine bay (South African southern Indian Ocean), and Moreton Bay (the Australian western Pacific) (Table 1). All these macrobenthic assemblages were sampled using essentially the same methodology, involving series of core samples each of 0.0054 m^2 area (except at the North Sea site where they were of 0.0027 m^2) and 100 mm depth. All sites were in continuous swards of seagrass, and were at least 10 m away from any interfaces with adjacent bare sediment. Intertidal samples were collected at low tide before complete tidal ebb whilst the substratum was still covered by at least 15 cm of water, and the subtidal ones by snorkelling. Cores were gently sieved ('puddled') through 710 μm mesh on site. This sampling procedure collects the smaller (mostly <5 mm) and more numerous members of the macrofauna that constitute the large majority of invertebrate biodiversity (Bouchet et al. 2002, Albano et al. 2011), though not the meiofauna nor much scarcer megafauna nor sessile animals attached to the seagrass leaves. Warwick et al. (2006) have shown that different patterning rules may apply to meiofauna and macrofauna, and likewise Davidson et al. (2004) and Leopardas et al. (2014) to sessile species. Sessile or semi-sessile species that had accidentally become detached from the seagrass leaves during sampling were therefore ignored.

Retained material from each core was: (i) placed in a large polythene bag or bucket of local sea water within which all seagrass was shaken vigorously to dislodge all but sessile animals; (ii) then re-sieved and transported immediately to a local laboratory, and (iii) there placed in a 30 × 25 cm tray over a light source in which the living fauna was located by visual examination using 3.5× magnifying spectacles until no further

Table 1
The 12 seagrass macrofaunal datasets analysed.

Seagrass species	Mean macrofaunal density m^{-2}	Mean % species occupancy	Assemblage patchiness (Lloyd's I_p)	Number of macrofaunal taxa	Number and size of core samples	Habitat type
'Goompi', Moreton Bay, Queensland, Australia (27°29′32″S,153°23′50″E) (Barnes, 2020)						
Cymodocea serratula	2309	11	1.128	83	45 × 0.0054 m^2	marine LWS
Halodule uninervis	2374	10	1.109	94	45 × 0.0054 m^2	marine LWS
Halophila ovalis	2008	9	1.139	82	45 × 0.0054 m^2	marine LWS
Zostera muelleri	2593	11	1.100	87	45 × 0.0054 m^2	marine LWS
'Dunwich', Moreton Bay, Queensland, Australia (27°29′22″S,153°24′24″E) (Barnes, 2014)						
Zostera muelleri	2291	5	1.119	143	150 × 0.0054 m^2	marine MLW
'Scolt Head', North Sea, UK (52°59′06″N,00°40′41″E) (Barnes and Ellwood, 2011)						
Zostera noltei	65,680	24	1.132	28	80 × 0.0026 m^2	marine HWN
Knysna estuarine bay, Western Cape, South Africa: 'Thesen' Islands residential Marina (34°02′59″S,23°02′54″E) (Claassens and Barnes, unpubl.)						
Zostera capensis	49,645	24	1.489	70	24 × 0.0054 m^2	subtidal marina canal
Knysna estuarine bay, Western Cape, South Africa: 'Brenton' (34°03′41″S,23°02′60″E), 'Steenbok' (34°03′36″S,23°02′06″E) and 'Belvedere' (34°02′54″S,23°00′01″E) (Barnes and Claassens, 2020)						
Zostera capensis	32,066	21	1.605	56	32 × 0.0054 m^2	subtidal marine
Zostera capensis	23,125	11	1.984	64	32 × 0.0054 m^2	subtidal marine
Zostera capensis	4780	23	1.072	41	32 × 0.0054 m^2	subtidal lagoonal
Knysna estuarine bay, Western Cape, South Africa: 'Crabs Creek' (34°02′02″S,22°59′39″E) and 'Kingfisher Bay' (34°03′39″S,23°03′09″E) (Barnes, 2019a)						
Zostera capensis	952	24	1.226	27	102 × 0.0054 m^2	estuarine MLW
Zostera capensis	2611	11	1.088	74	325 × 0.0054 m^2	marine MLW

animal could be observed. Animals were identified to species level wherever possible, with all organismal nomenclature here being as listed in the World Register of Marine Species (www.marinespecies.org) (accessed June 2020). It should be noted, however, that the specific identity of several animals in the Knysna and Moreton Bay samples, especially amongst the Polychaeta and Peracarida, is questionable because of lack of relevant recent systematic studies; those of Polycladida, Oligochaeta and Nemertini, and many members of other groups less than 3–4 mm in largest dimension, are virtually unknown. Such animals were treated as morphospecies, an operationally appropriate procedure to detect spatial patterns in numbers of species and their differential abundance (Dethier and Schoch, 2006; Gerwing et al., 2020). As the earlier work on intertidal seagrass at Knysna (Barnes, 2019a) considered only the more dominant species at each site, two of those sites were also reworked to include the whole macrobenthic assemblages there.

All abundance data are given as densities (numbers m^{-2}) and for individual species calculation of mean densities included unoccupied samples (i.e. zero values); occupancies are proportions of the total samples at a given site in which a species was present and correspondingly unoccupancies are those from which it was absent. Species occurring at a site only in the form of singletons or doubletons were deleted from its dataset. Magnitude of patchiness was ascertained by spatial point pattern analysis of count data using Lloyd's index of patchiness (Lloyd, 1967), $I_p = [1 + 1/k]$, where k is the dispersion parameter of the negative binomial distribution, i.e. $= [1 + (v-m)/m^2]$, where 'm' is the mean abundance across samples and 'v' is the associated spatial variance (Waters et al., 2012; Henriques et al., 2017). This index, that indicates the number of times as crowded an individual organism is, on average, than it would have been if the same population had been distributed randomly, has been demonstrated to yield equivalent results to those of the spatially-explicit Moran's spatial autocorrelation index for intertidal dwarf-eelgrass macrobenthos (Barnes and Hamylton, 2019). It is also independent of sample size over a wide range of areas, provided that the animals position themselves at random with respect to each other within a patch and that the patches are large relative to sample size (Lloyd, 1967; Myers, 1978). Granted that the core area was ≤ 0.0054 m^2, it seems unlikely that macrofaunal patches were smaller than that; indeed Barnes (2016) had previously found at a Knysna seagrass site that cores of 0.0015, 0.0026 and 0.0054 m^2 spatial grain all produced the same value of the closely-similar but differently-derived Morisita's I_δ index (the scaled probability that two points chosen at random from the whole population will be present in the same sample). It should be noted that Lloyd's I_p although termed an index of *patchiness* is actually an index of *dispersion*, which may not be that relevant a distinction in that most if not all habitats and organisms display patchy or aggregated dispersions (Wiens, 1976; Azovsky et al., 2000; Lundquist et al., 2010). However, it does mean that values of such an index that indicate significant departures from random in the direction of patchiness (i.e. $I_p > 1$) or regularity ($I_p < 1$) are dependent on the total number of individuals in the dataset, which will vary from species to species and across sites. Hence *significant* departures from random in the direction of patchiness *per se* cannot be associated with any specific value of the index.

Because patchiness is reflected by both distribution and abundance, indices of patchiness such as I_p will be influenced by two separate phenomena (albeit that one is only the limiting state of the other): (a) proportion of samples in the dataset in which a given species is not represented (i.e. levels of unoccupancy); and (b) magnitude of variation in abundance across those samples in which it is present. Therefore, besides calculation of the I_p index itself, these two influencers were also assessed in parallel, variation in spatial abundance across only occupied samples by Lloyd's domain-free index of mean crowding (I_c), where $I_c = m + (v/m - 1)$ (Lloyd, 1967; Bez, 2000), described by Wade et al. (2018:1225) as 'one of the most versatile tools available to biologists'. Using the same abundance parameters as I_p and I_c, conformity of the data with the expression of He and Gaston (2003) and Gaston et al. (2006) uniting abundance, occupancy and spatial variance, i.e. $1 - (m/v)^{(m^2/(v-m))}$, was also tested, as was, for comparison with the Lloyd indices, Morisita's I_δ index (Morisita, 1959, 1962), which is also much used in benthic marine ecology, both in its original formulation, $n(\Sigma x_i^2 - \Sigma x_i)/(\Sigma x_i(\Sigma x_i - 1))$ where n is the number of core samples and x_i is the number of individuals in 'i'th sample, and in the Smith-Gill (1975) standardised version constrained to vary between −1 and +1. Correlations between metrics are given as Spearman's rank coefficient, S_r. All calculations were carried out in Microsoft Excel for Mac 16.37 with the StatPlus:mac Pro 7.1.1 add-on, or via *PAST* 3.24 (Hammer et al., 2019); curves were fitted using KaleidaGraph 4.5.4; and statistical significance of any detected patchiness (i.e. for $I_P > 1$) was determined by Monte Carlo simulation using 9999 iterations.

3. Results

It was apparent in all plots of log patchiness versus log abundance or log occupancy that individual species clustered in two different sets (Fig. 1). One set comprised all those uncommon species represented by only 0 or 1 individual in each sample at a site, for which therefore $\Sigma x_i^2 = \Sigma x_i = n$ where n is the number of samples in which it was present. These species comprised 11–46% (mean 27.5%) of the total number, displayed small levels of I_p (≪1) and contributed nothing to the study, both abundance and occupancy automatically showing a linear relationship with patchiness at each site. Analysis was therefore restricted to those more abundant species in the second group, i.e. to all those represented by >1 individual in at least one sample at a site. In all such cases observed levels of occupancy were effectively exactly as predicted by the spatial abundance parameters (He and Gaston, 2003; Gaston et al., 2006), i.e. from the observed intraspecific mean values of abundance and the associated spatial variances (Fig. 2).

The four seagrass genera at Goompi (Fig. 3), the four intertidal stands of *Zostera* (*Zosterella*) species (Fig. 4), and the four subtidal stands of *Z. capensis* at Knysna (Fig. 5) all showed the same basic inverse relationship of patchiness, as assessed by Lloyd's I_p, to occupancy. This was significant in all but the subtidal Belvedere site at Knysna, where it was nevertheless close to significance at $P = 0.06$. The relationships broadly conformed to a power law with a mean exponent of −0.76 (SE 0.04), although the data were highly scattered (coefficient of determination,

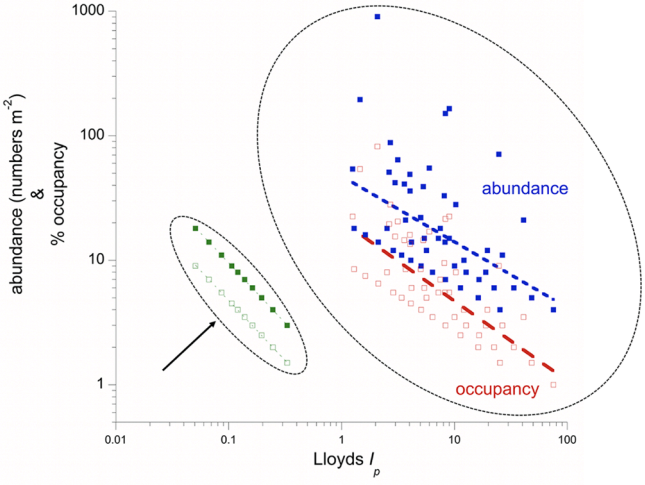

Fig. 1. Representative interspecific patchiness-occupancy and patchiness-abundance relationships showing the separate distribution of those relatively uncommon species that do not occur in excess of 1 individual animal in any individual sample (arrowed) (data from Barnes and Barnes, 2012, for several sites along the North Stradbroke Island coast, Moreton Bay, Queensland). Such species are not included in Figs. 3–6 below.

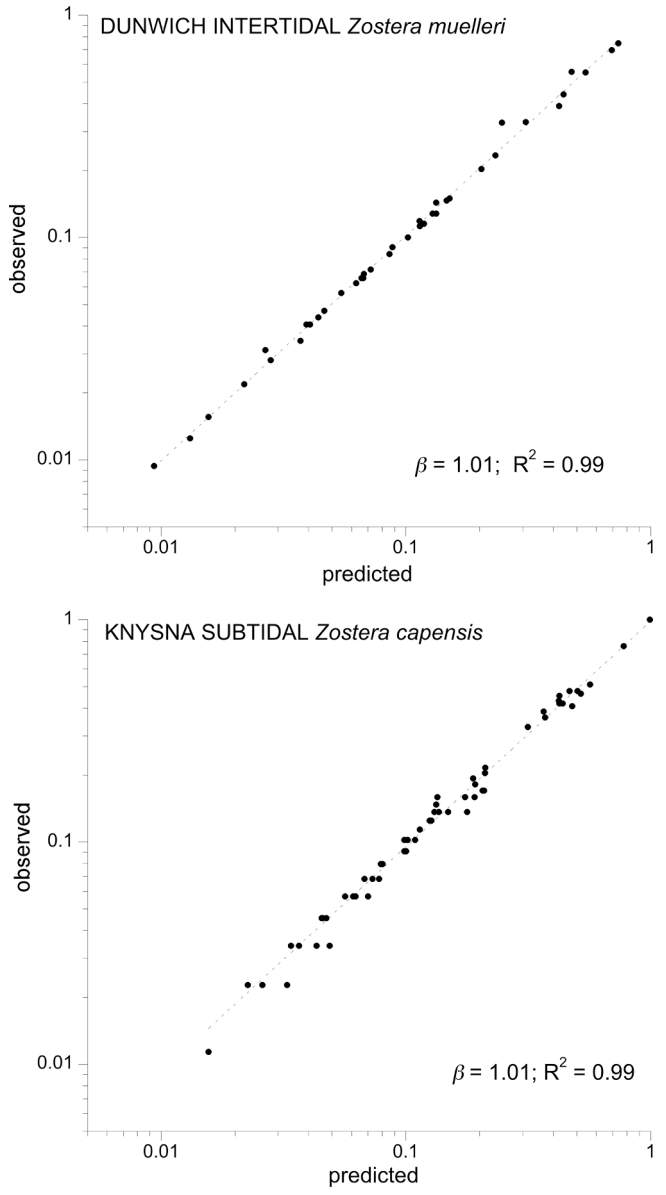

Fig. 2. Two examples of the extremely close agreement between observed levels of occupancy in the interspecific seagrass macrobenthic data and those predicted by the expression of He and Gaston (2003) and Gaston et al. (2006) involving only the abundance metrics mean (m) and variance (v), i.e. $1 - (m/v)^{(m^2/(v-m))}$.

$R^2 < 0.50$, mean 0.30). Slopes of the relationships differed significantly between sites (ANCOVA $F = 4.09$; $P < 0.004$) but with such low values of R^2 little reliance can be placed on the rank order obtained. The values of R^2 for the corresponding abundance-occupancy relationship at the same sites, for example, were >0.74 (mean 0.89). The correlation of patchiness and abundance was also always negative but was significant at only eight of the 12 sites plus two that were close to significance at $P = 0.06$. The mean power-law exponent at sites where the relationship was statistically significant was −0.80 (SE 0.08), but again with considerable scatter ($R^2 \leq 0.30$, mean 0.13). Across individual sites there was a marginally significant correlation between the abundance and occupancy scaling coefficients (S_r 0.65; P 0.04), but no significant relationship with either coefficient and overall abundance or species density.

Correlations of Lloyd's I_c values with those of I_p were only half the magnitude of those between I_p and unoccupancy, and 6 out of the 12 did not achieve significance. Although all were positive, it was notable that correlations of I_p and I_c varied markedly (S_r 0.06–0.65), the variation cutting across the Goompi locality such that of the *Cymodocea* bed was not significant (S_r 0.34, P 0.11) whilst those of the other three genera were ($S_r > 0.48$, $P < 0.02$). No subtidal bed at Knysna, however, showed a significant correlation between the two ($S_r < 0.32$, $P > 0.13$). With one exception (the species-poor, high mean occupancy Scolt Head site), the expression [a.unoccupancy + $(1-a).I_c$] showed higher levels of correlation with I_p than with unoccupancy alone (Fig. 6); values of a lying within the range of 0.825–0.950 ($S_r > 0.82$, $P \ll 0.00001$), so that all evidence indicated that variation in abundance at occupied sites was a very minor influencer of patchiness, even when, as in the Thesen Islands marina, values of mean crowding across component species of the macrofauna ranged from <0.3 to> 380. For reasons set out in the Materials and Methods section above, statistically significant patchiness of any given species *per se* cannot be read directly from Figs. 3–5. In general, however, all values of $I_p > 1.5$ (SE 0.1) indicate statistically significant patchiness ($P < 0.05$).

Both the index of dispersion and Lloyd's indices are based on the two abundance metrics, variance and mean, and it is notable that whereas Lloyd's I_p showed a consistent negative relationship with both occupancy and abundance, the index of dispersion (both as v/m and its log v/log m form) showed no such relationship, from site to site varying from being significantly positively correlated to significantly negatively so with each metric, although at the majority of sites there were no significant correlation (see Fig. 7). As expected, the corresponding values of Morisita's I_δ were always almost perfectly correlated with those of Lloyd's I_p ($S_r > 0.996$), although the standardised version was slightly less so at $S_r < 0.91$. The standardised Morisita index also showed considerably lower levels of correlation with both abundance and occupancy ($S_r < -0.45$), though across all sites it was strongly correlated with I_c ($P < 0.01$) unlike the other indices.

The large majority of macrofaunal species in the seagrass beds investigated feed at or above the sediment surface, but many live in tubes or burrows below the surface. Information on the biology of most of them at the investigated localities is not available but based on what is known and on that available on related species in compilations such as Macdonald et al. (2010), it is possible to categorise them as 'epifaunal' (including living on the surface itself) or 'infaunal', a division that often has far reaching implications for their spatial ecology (Reiss et al., 2010; Silberger et al., 2019). On that basis the various sites clearly fell into two groups in terms of their occupancy and abundance. Across the Goompi sites, the mean occupancy of infaunal species was greater than that of epifaunal ones at each of the four sites (overall 17.4% vs 9.6%) (one-way ANOVA $F_{1,52} = 4.2$; $P < 0.05$), as was their mean abundance (48.8 vs 26.8) although not significantly so. The reverse was true at five of the temperate sizes (the four subtidal at Knysna and one on Scolt Head): subtidally in the marine embayment at Knysna, for example, mean infaunal density and occupancy were 60 m^{-2} and 15% whereas those of the epifauna were 1200 m^{-2} and 24% occupancy (ANOVA $P < 0.02$ in both cases).

These differences mirror marked compositional differences between the warm-temperate subtidal and cool-temperate intertidal macrobenthos on the one hand and the warm-temperate and subtropical intertidal faunas on the other. Overall at subtropical Goompi, the most abundant species comprised <25% of the total numbers, and decapod crustaceans, polychaetes and amphipods comprised approximately equal numbers in the group of ten most numerous species. Similarly, in the warm-temperate Knysna intertidal macrobenthos no one species dominated, at Kingfisher, for example, the most abundant species comprised <12% of the total and 20 annelids (19 polychaetes and an oligochaete), 12 peracaridan and six decapod crustaceans together contributed 80% of the total numbers. In contrast, all five warm-temperate sites at subtidal Knysna and intertidal Scolt Head were heavily dominated by a single, epifaunal, microphytobenthically-feeding microgastropod, i.e. by the cerithioid *Alaba pinnae* at Knysna (83% of total numbers, and a mean I_c of 300), and by the truncatelloid *Peringia ulvae* on Scolt (79% of the total, and an I_c of 166 for a spatial

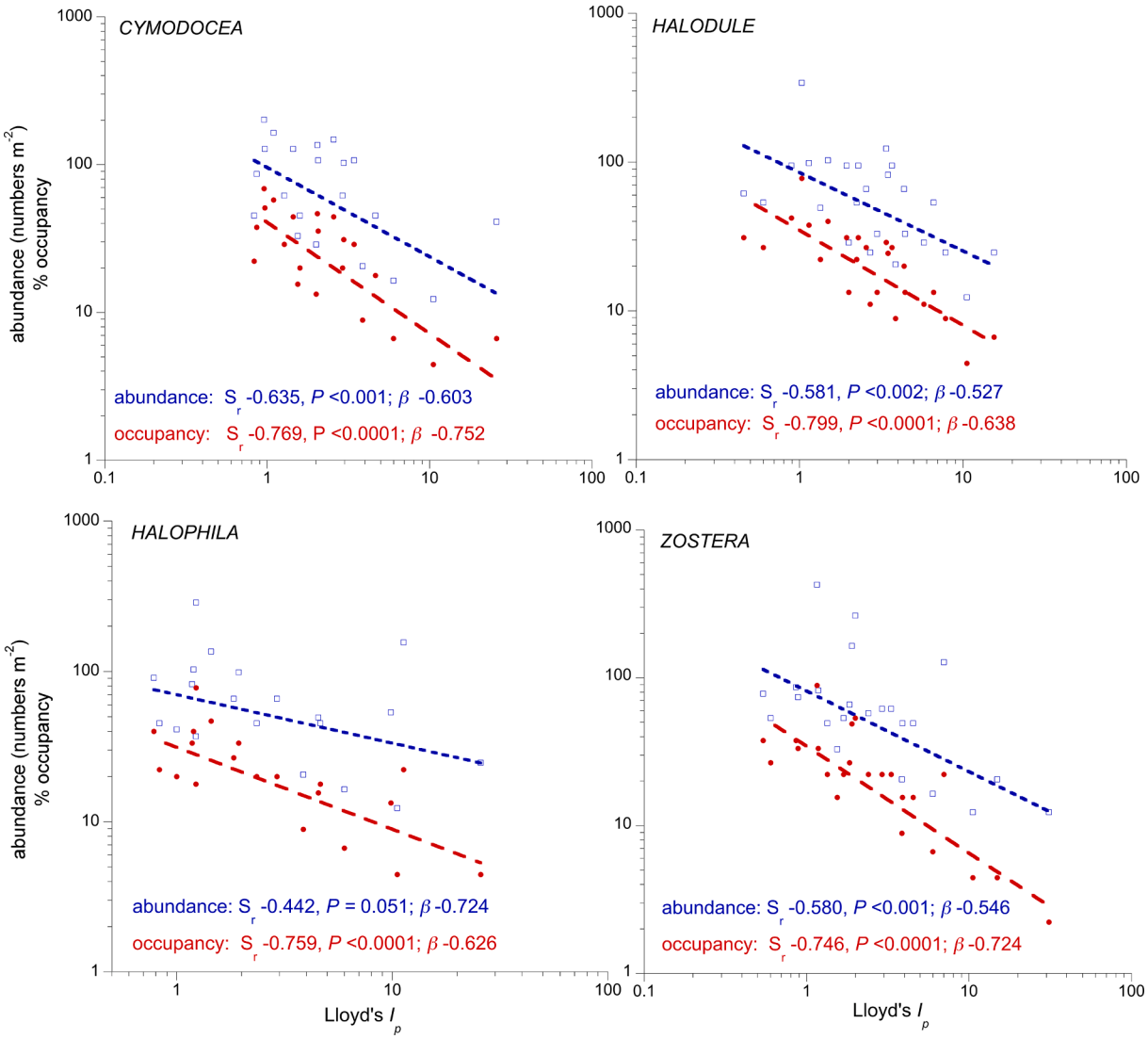

Fig. 3. Interspecific patchiness-occupancy and patchiness-abundance relationships of the benthic macrofauna of monospecific stands of four different seagrasses at low water spring tide level off the township of Goompi, Moreton Bay coast of North Stradbroke Island, Queensland. Values (S_r) and statistical significance (P) of correlations, and values of the scaling coefficient of the fitted power-laws (β) are given.

grain of only 0.0027 m^2). Although the species comprising both the microgastropod-dominated assemblages displayed the usual high correlation between their abundance and occupancy ($S_r > 0.97$; $P \ll 0.00001$), the relationship (Fig. 8) departed from those demonstrated earlier for intertidal Knysna (Barnes, 2019a) and low water spring Goompi (Barnes, 2020) in being curvilinear ($R^2 > 0.96$) rather than linear, in part consequent on the presence of the superabundant snails and the resultant very large range in total abundance of the component species (Steenweg et al., 2018). On the basis of the pool of the 15 most patchy species at each of the 12 sites, however, there was no significant difference (one-way ANOVA $P > 0.08$) between the values of I_p or I_c for epifaunal versus infaunal species.

4. Discussion and conclusions

The seagrass macrobenthic assemblages under consideration here hailed from three different oceans, spanned a climatic range from cool temperate to subtropical, included systems of from high (>200 m^{-2}) to low (<30 m^{-2}) species density, high (>60,000 ind. m^{-2}) to low (<3000 ind. m^{-2}) overall abundance, and high (>20%) to low (<12%) average occupancy. They inhabited regions ranging from permanently submerged subtidal zones to those above mean sea level experiencing long periods of aerial exposure, lived in stands of four different genera of seagrasses varying in form from lush dense meadows of >1 m long leaves to short turfs of <5 cm, and were subject to environmental conditions ranging from fluctuating estuarine brackish to constant full-strength coastal sea water. The assemblages varied from infaunal- to epifaunal-dominated, and from being overwhelmingly dominated by one single species to displaying a much more broad and equitable series of co-dominants.

Nevertheless, the present study showed that all investigated seagrass macrobenthic assemblages shared a very similar abundance-occupancy-patchiness relationship. As the highly correlated abundance and occupancy of the macrobenthic species increased, so did their patchiness decrease: the more abundant and widespread species displayed the least patchiness. Earlier results from intertidal seagrass assemblages at Knysna did not show significant abundance-patchiness correlations (Barnes, 2019a), although that study was devoted only to the most common and abundant species (those achieving occupancies >10% and/or abundances >50 m^{-2}). The present work included all except rare species, but it was still the case that not all abundance-patchiness correlations proved significant, although most did, including for the two intertidal stands at Knysna that were re-investigated. The relationship of patchiness with occupancy clearly proved much the stronger of the two

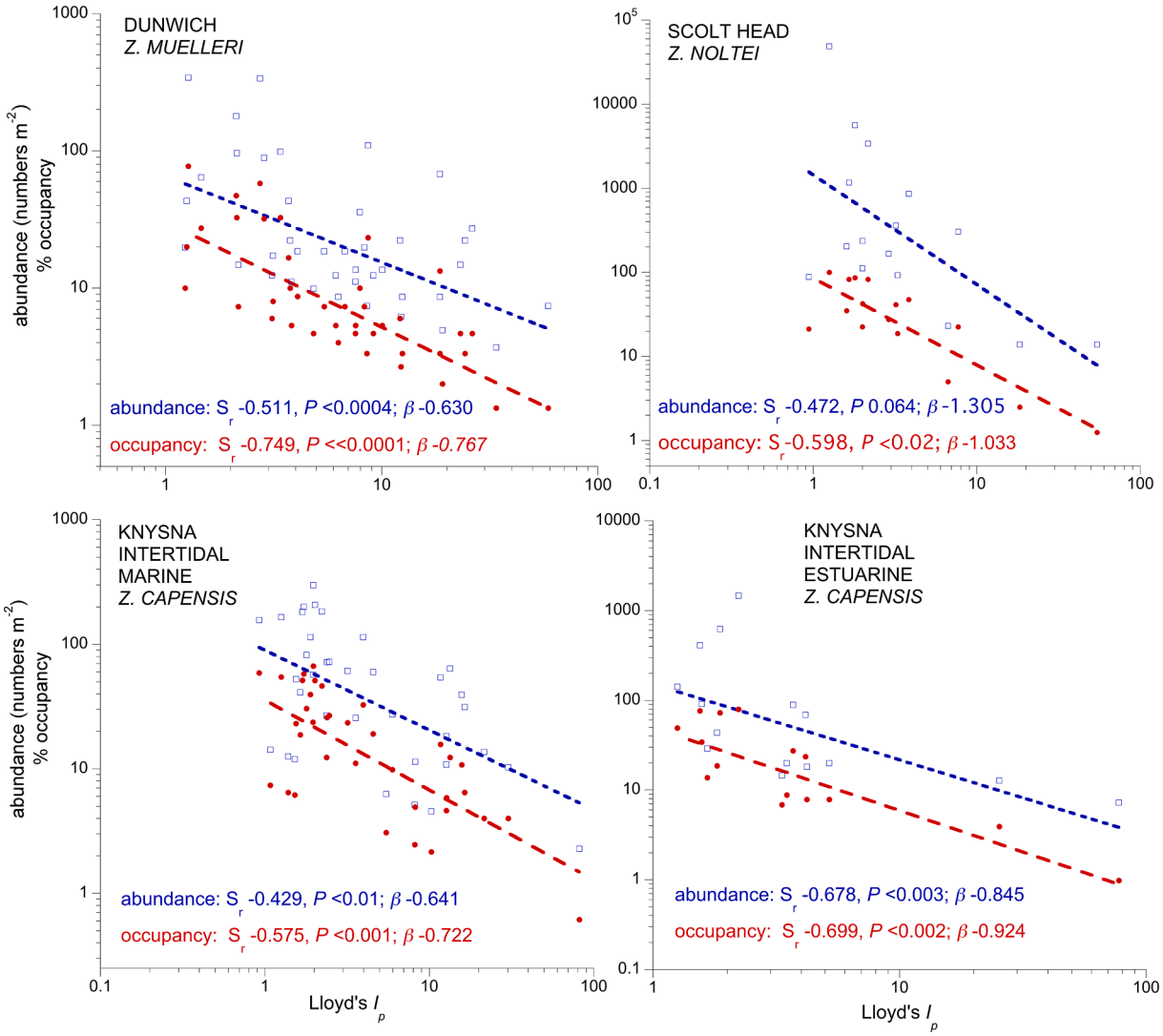

Fig. 4. Interspecific patchiness-occupancy and patchiness-abundance relationships of the benthic macrofauna of intertidal meadows of three species of the dwarf-eelgrass *Zostera* (*Zosterella*): *Z.* (*Z.*) *muelleri* at mean low water level (MLW) at Dunwich, Moreton Bay, Pacific Ocean; a high-intertidal *Z.* (*Z.*) *noltei* bed on Scolt Head Island, North Sea, Atlantic Ocean; and two beds of MLW *Z.* (*Z.*) *capensis* at Knysna on the South African Indian Ocean coast, one from Kingfisher Bay in the marine embayment and the other from Crabs Creek in the lower estuary.

in all cases; and in seagrass macrobenthic assemblages at least, the extent of unoccupancy across an area has a much stronger effect on degree of patchiness than does variation in density across those sites at which a species does occur.

These macrobenthic seagrass assemblages also known to share a number of other ecological characteristics. Previous analysis of the intertidal *Zostera* macrofaunas disclosed that they all exhibit species densities that do not depart from those to be expected under a null model of independent assortment of members of the available species pool granted their overall frequencies of occupancy (Barnes, 2013, 2014; Barnes and Barnes, 2014). This in turn suggests that such assemblages are held well below the level at which the individual species might interact competitively with each other, most probably as a result of the top-down control exerted by all the juvenile prawns and fish that use them as nursery grounds (e.g. Beseres and Feller, 2007; Whitfield, 2017). This includes the temperate intertidal Scolt Head and Knysna sites and therefore stands counter to the suggestion of Freestone et al. (2020) that predation does not shape temperate seagrass assemblages, only tropical ones, although other evidence does certainly point to its greater impact in low-latitude seagrass systems (Barnes, 2010).

Further, local patchiness of these assemblages (i.e. across areas of <1 ha) is not only spatially constant down to scales of 0.1 m^2 at a low but statistically significant level (Barnes and Laurie, 2018; Barnes and Hamylton, 2019), possibly as a result of the type of optimal foraging by epibenthic predators described by Beseres and Feller (2007), but Lloyd's I_p values for whole intertidal seagrass macrofaunal assemblages seem remarkably uniform across both geographical space (Barnes, 2019b) and seagrass species (Barnes, 2020). Recorded values for assemblages associated with dwarf eelgrasses [*Zostera* subgenus *Zosterella*] at 33 sites of South African *Z. capensis*, Australian *Z. muelleri capricorni* and UK *Z. noltei* are 1.125 ± 0.054 (SD) (Barnes, 2019b; Barnes and Hamylton, 2019), whilst those from intertidal Australian *Cymodocea*, *Halophila* and *Halodule* all also fall within 1 standard deviation of that mean (Barnes, 2020). Those of subtidal dwarf eelgrass (only examined to date in *Z. capensis* at Knysna), however, lie outside this range, being considerably larger at a mean value of 1.46 (Barnes and Claassens, 2020) as indeed do those of such adjacent sandflats and mangrove fringes as have been investigated (Barnes, 2020).

Because of potential independent variation in (a) numbers of high-density hot-spots per unit area, (b) the individual areal extent of such patches, and (c) their intensity (Kraan et al., 2009), and because of its hierarchical spatially-nested nature (Kotliar and Wiens, 1990; Morrisey

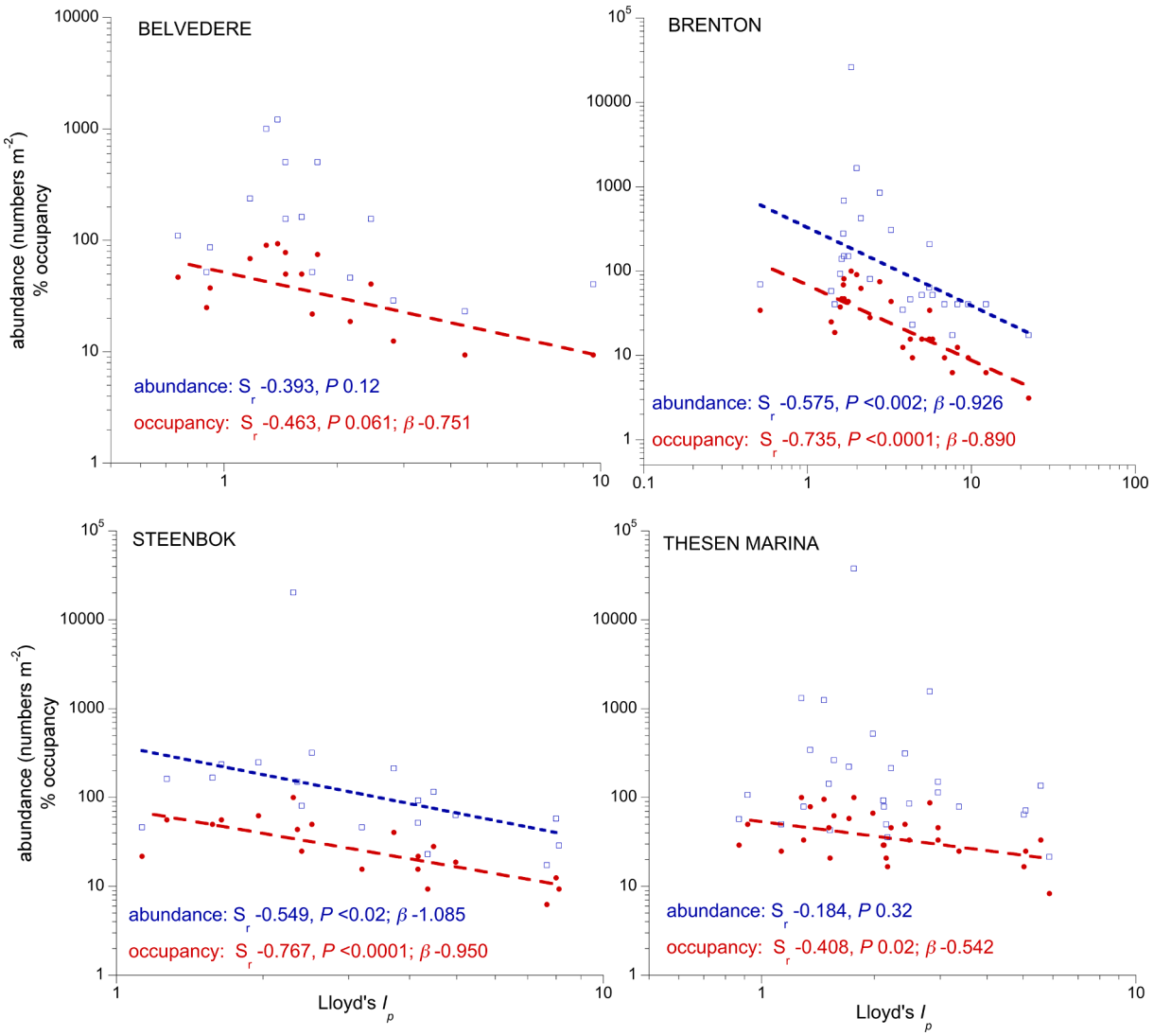

Fig. 5. Interspecific patchiness-occupancy and patchiness-abundance relationships of the benthic macrofauna in four subtidal beds of *Zostera* (*Z.*) *capensis* in the Knysna estuarine bay, South Africa: Belvedere in the lagoonal reach; Brenton and Steenbok in the marine embayment; and Thesen in the artificial canals of the Thesen Islands Marina in the same embayment.

et al., 1992), patchiness is far from being a simple uniform concept, and its causes, particularly across small scales, are poorly understood (Gutt et al., 2019) and probably complex (Reise, 1979; Kotta and Möller, 2009). Methods to assess it may each highlight only one of these potential aspects or indeed may run the risk of confusing the study of processes giving rise to its different aspects by combining them into a single 'magic number' (Reise, 1979; Barnes and Hamylton, 2019), equivalent to the problems associated with the separate features of species richness and equitability of abundance in the concept [or 'non-concept' (Hurlbert, 1971)] of 'species diversity' (Barrantes and Sandoval, 2009). Presence/absence, however, is a fundamental aspect of most notions of patchiness. Indeed, in many studies of patchiness of the seagrass vegetation itself, as of other habitat patchiness, it appears to be *the* fundamental aspect. The two potential influences of unoccupancy and differential density when present were separated in the present study, and the clear bias of Lloyd's I_p (and of the cognate Morisita's I_δ) in the direction of unoccupancy therefore does not seem inappropriate. Although the (sometimes large) variation in mean crowding was a relatively insignificant influencer of patchiness, the two expressions unoccupancy and I_c together permit calculation of an expression closely and highly significantly correlated with interspecific I_p, again suggesting that I_p, although a single magic number and, like other spatial point pattern analyses, the subject of potential criticism (e.g. Hayes and Castillo, 2017), does have real practical value.

Although in all cases studied to date (Barnes, 2019a; present paper), patchiness and occupancy of the macrobenthic seagrass assemblages showed (or almost showed) a significant negative relationship, both at the scale of individual sites of <1 ha through to whole sections of an estuarine bay, the relevant R^2 values are nowhere near those of the associated relationship between occupancy and abundance (although Bijleveld et al., 2018, obtained some very low values of R^2 for that relationship in some of the Dutch Wadden Sea macrobenthos). This very considerable scatter of data points, in several cases including frequent extreme outliers, might be consequent on relatively few species in total in some faunas, and on ecological inducers of patchiness that may act independently of those determining occupancy, including predation (Nachman, 2006; Freestone et al., 2020; etc.), patterns of recruitment of juveniles (Foggo et al., 2007; Palardy and Witman, 2014), and those relating consumers to the availability of unevenly abundant specific types of resource (Grünberg, 2012). As yet, this scatter of points representing the individual species renders attempts to explain potential differences in the slopes of overall interspecific relationships across sites impossible.

The subtropical Australian sites all displayed very low macrofaunal

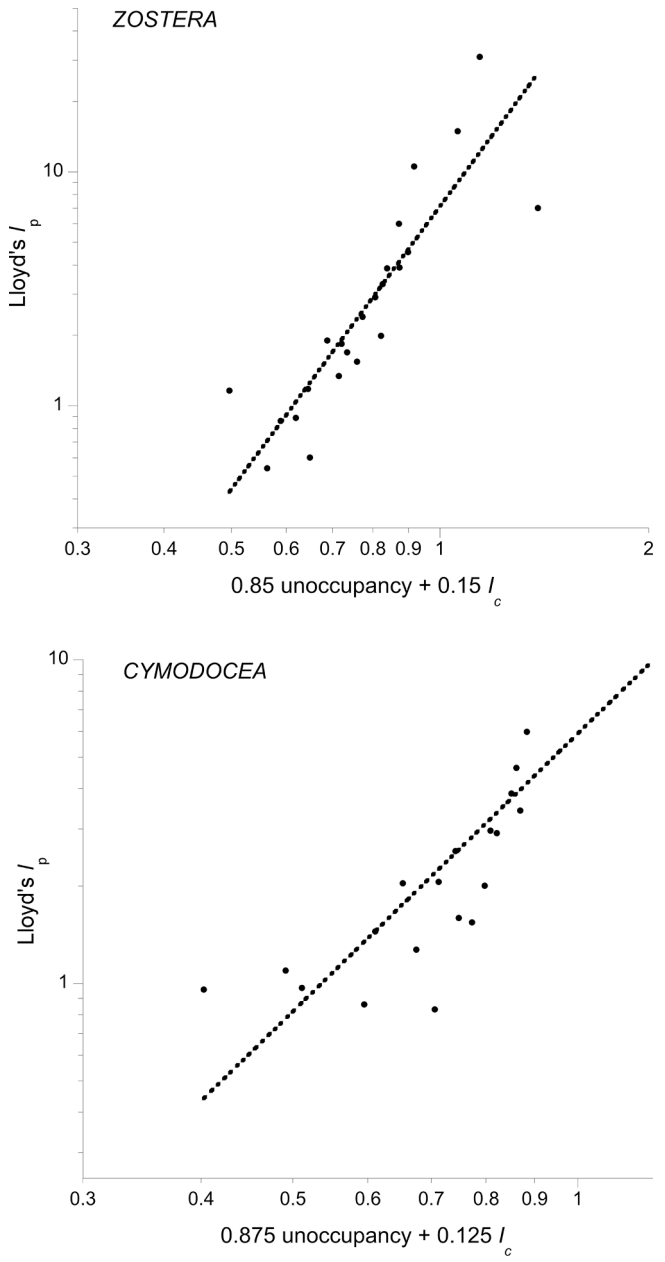

Fig. 6. Relationship between patchiness (Lloyd's I_p) and both proportional unoccupancy and mean crowding (Lloyd's I_c) in the *Cymodocea serratula* (S_r = 0.931, $P \ll 0.00001$; $R^2 = 0.93$) and *Zostera muelleri* macrofaunas at Goompi (S_r = 0.951, $P \ll 0.00001$; $R^2 = 0.29$).

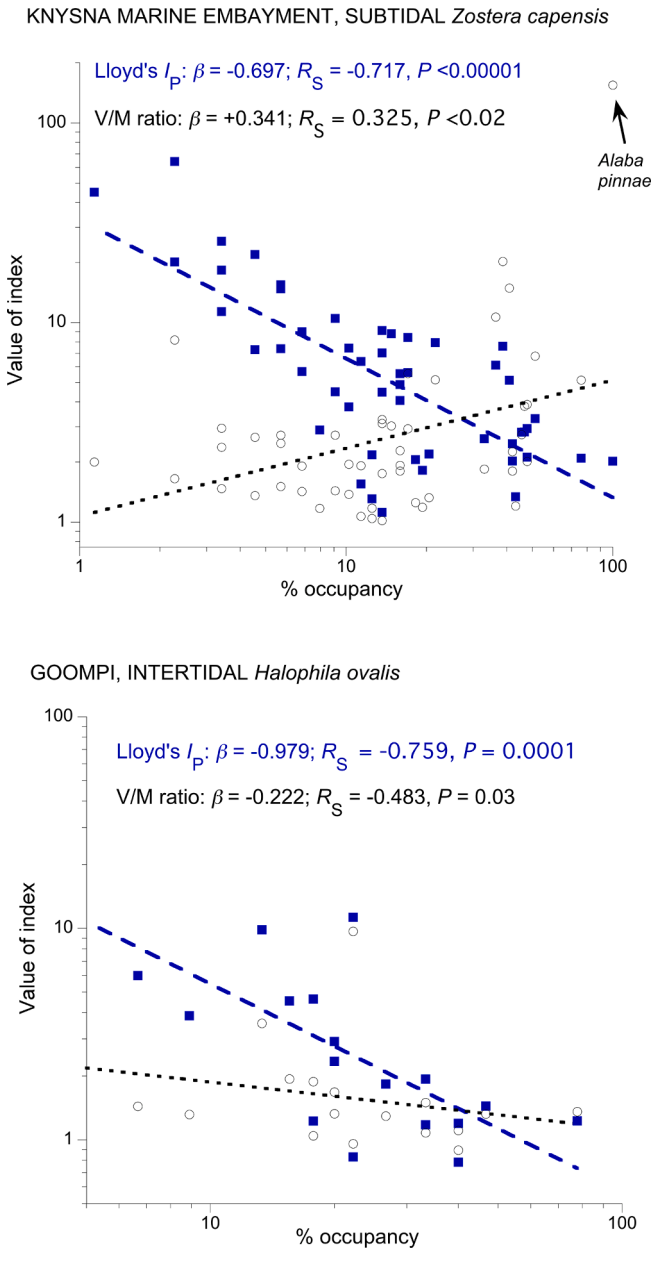

Fig. 7. The differential relationship of two indices of dispersion to occupancy in the seagrass macrobenthic data. In all assessed cases, Lloyd's index of patchiness I_p was negatively correlated with occupancy, whereas the interspecific ratio of spatial variance to mean abundance varied from being positively correlated (as in the Knysna *Zostera*), through no significant relationship (as at most sites), to negative correlation (as in the Goompi *Halophila*). The outlier of *Alaba pinnae* in the subtidal Knysna seagrass is there both by far the most abundant and widely distributed species.

densities, equivalent to <5% of those of the comparably-sized macrofaunal species at several temperate seagrass sites. If it really is the case, as this and their stochastic species-composition above seem to confirm, that at least those (and possibly all) seagrass macrofaunal assemblages are maintained below their potential carrying capacity, including as a result of the heavy predation exerted by juvenile nekton using seagrass as a nursery area and by all the resident infaunal and epifaunal predators, this will have marked repercussions on potential causes of the seagrass abundance-occupancy-patchiness relationship. In effect all those arguments relying on density-dependent processes would appear somewhat unlikely, as do those involving siting near the margins of ranges (except possibly the Knysna Crabs Creek site). All the studied areas of seagrass, however, and particularly those in Morteton Bay, form part of much larger systems, and hence putative causal effects involving potential movements within a metapopulation cannot be ruled out. At the simplest level, rare species are almost by definition patchy and the argument put forward linking large occupancies to large abundances (see, e.g., Gaston et al., 2000) can be easily extended to include associated low levels of patchiness. This could apply to a number of the dominant species, though clearly not to species such as *Circulus* and *Pseudoliotia* below. Unfortunately, many explanations rely on an adequate knowledge of the niches of the species involved, and that is sadly lacking for many seagrass systems.

This is well illustrated by the biofilm-feeding, epifaunal microgastropods that dominate some sites at all three geographical localities investigated: a pattern of dominance that may be related to their relative avoidance by consumers (Reynolds et al., 2018), not least because of low

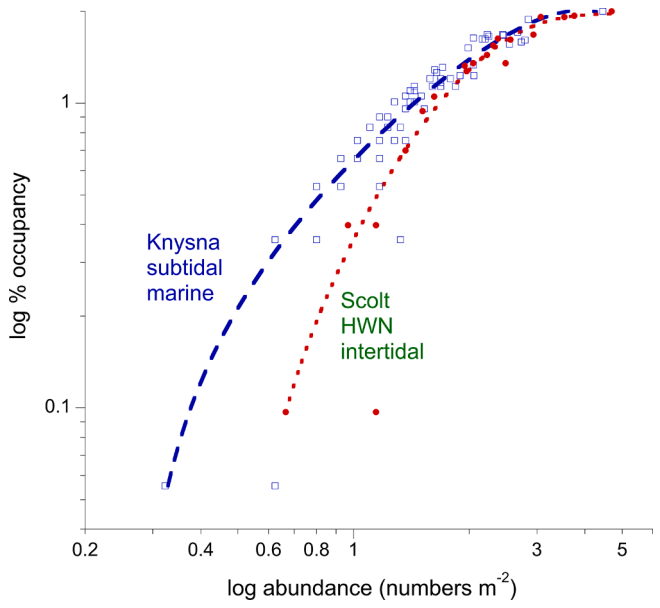

Fig. 8. Curvilinear interspecific abundance-occupancy relationships in the seagrass macrobenthos of *Alaba*-dominated subtidal meadows of *Zostera capensis* in the marine embayment of the Knysna estuarine system, South Africa, and in that of *Peringia*-dominated *Zostera noltei* beds on the high-level intertidal mudflats of Scolt Head Island on the British North Sea coast, where ranges in abundance attain 30,000 and 50,000 m^{-2} respectively.

palatability (Vinson and Baker, 2008). The relatively well-known hydrobiid *Peringia ulvae* that is the major component of the Scolt Head seagrass fauna at an average density of 50,000 m^2 is the exception in being much researched and hence being quite well known (e.g. Araújo et al., 2015); the almost equally abundant litiopid *Alaba pinnae* of the subtidal Knysna seagrass (at a mean 30,000 m^2), however, is almost completely unknown (Barnes and Claassens, 2020). Both are outliers, not only because of their extreme abundance but also because in their respective areas they are the only species to have an occupancy of 100%; no other species, except on Scolt the tubificid *Tubificoides benedii* and at one Knysna site the trochid *Gibbula cicer*, gets even close to this figure. *Alaba*, however, appears largely restricted to the seagrass leaves and does not occur on the sediment surface, whilst *Peringia* is equally, if not more, abundant there. Seemingly equivalent species, especially the calopiid *Calopia imitata*, form part of the group of co-dominants at the Moreton Bay sites, but *C. imitata* only achieves an average density of some 500 m^{-2}. Others, such as the <5 mm vitrinellid snail *Circulus cinguliferus* which was the most patchy species at the Deanbilla site of Barnes and Laurie (2018) are only very locally abundant. *Circulus* had an unoccupancy of 91% but overall was one of the most abundant species at >60 m^{-2}. Nevertheless, because 57% of its numbers occurred in only two 0.0054 m^2 samples (<0.8% of the total) and 44% in just one, it also forms an extreme outlier. Likewise, the slightly smaller vitrinellid *Pseudoliotia speciosa*, which was the fifth most abundant species overall at Dunwich, had an unoccupancy of 80%, but <12% of the samples in which it did occur contributed 38% of its total numbers. Yet further apparently equivalent litiopid, rissoid, elachisiniid, scaliolid and dialid microgastropods at Dunwich and nearby localities are just as characteristic of seagrass beds but only occur at occupancies of <1.5% and abundances of <4 m^{-2} (Barnes, 2019c), and so form part of the group of species that are rare by any standards (Gaston, 1994; Benkendorff and Przeslawski, 2008) and for that reason were poorly represented in the datasets of this study. All such species are listed as microphytobenthic biofilm grazers and why some members of this guild are abundant and widespread dominants whilst most others are rare, even if for some locally plentiful, is completely unknown, as is why microgastropods dominate *Zostera* (*Zosterella*) faunas but not those of *Cymodocea* or *Halodule* (Barnes, 2020). Of course such general ignorance of the causes of rarity in animal assemblages is not restricted to microgastropods or to seagrass (Magurran and Henderson, 2003; Viole et al., 2017).

Equivalent data on abundance, occupancy and patchiness of seagrass macrobenthic species are not available for any other localities, although there are some data on overall abundance and numbers of species to suggest that at least in those respects the sites investigated here are not atypical. Like Scolt Head, other *Z. noltei* sites in the northeastern Atlantic are characteristed by species-poor but high abundance assemblages dominated by *Peringia ulvae*, *Tubificoides benedii* and *Pygospio elegans*, e.g. Sylt at 55°N (Reise, 1978) and Arcachon at 44°N (Blanchet et al., 2004). Klumpp and Kwak (2005) describe a species-rich, polychaete and crustacean dominated, *Cymodocea*, *Halodule* and *Halophila* meadow at Townsville in tropical Queensland (19°S) with macrofaunal densities within the same range as at Goompi; and faunas and their abundance at other South African localities, e.g. Langebaan (Puttick, 1977), and the Kariega (Hodgson, 1987) and Gamtoos (Schlacher and Wooldridge, 1996) estuaries, mirror those in various regions of the Knysna system. It is clearly desirable, however, that more sites and habitats dominated by other seagrass species, indeed more types of system as a whole, be examined to establish the generality of the patchiness-occupancy and patchiness-abundance relationships outlined here. In comparable systems with relatively few but very widespread species, e.g. some brackish-water habitats (Warme, 1971; Reizopoulou et al., 2014), it might be predicted that unoccupancy might cease to be the major influence on patchiness and variation in abundance as measured by Lloyd's I_c correspondingly become much more important. Patchiness might be a rather diffuse and nebulous concept but, although it is early days and the considerable scatter of individual datapoints requires further consideration, it does seem as if it might successfully be accommodated into the unified multivariate macroecological pattern discerned by He and Gaston (2003), at least empirically.

Author contributions

RSKB conceived, designed, and executed this study and wrote the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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